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The development of the embryo-sac and embryo of Potamogeton lucens

Melville Thurston Cook

(WITH PLATES 9 AND 10)

The purpose of this study was to compare the development of the embryo-sac and embryo of this plant with those of other well-recognized monocotyledonous plants and with the Nymphaeaceae; also for the purpose of comparison with Holferty's (9) paper on *Potamogeton natans* and Wiegand's (14) paper on *P. foliosus*. This became especially important since the two authors differed so widely in their conclusions concerning the development of the embryo-sac. My own results are somewhat different from either and it has been possible to carry the study of the embryo further. It, therefore, seems advisable to publish the results at this time.

The material for this study was collected in a large lagoon near San Antonio de los Baños in the Province of Havana, Cuba. It was killed and fixed in the following preparations:

1. Chromo-acetic solution,	
Water	99 c.c.
Glacial acetic acid	.3 c.c.
Chromic acid	.7 gram.
2. Picro-acetic solution,	
(*a*) Saturated aqueous solution of picric acid	99 c.c.
Glacial acetic acid	1 c.c.
(*b*) Saturated 70 per cent. alcoholic solution of picric acid	99 c.c.
Glacial acetic acid	1 c.c.
3. Sulphuro-acetic solution,	
(*a*) Saturated aqueous solution of picric acid	98 c.c.
Sulphuric acid	2 c.c.
(*b*) Saturated 70 per cent. alcoholic solution of picric acid.	98 c.c.
Sulphuric acid	2 c.c.

All these preparations were quite satisfactory but the picro-acetic preparations were the best and the aqueous solution better than the alcoholic.

The greater part of the work was done in the laboratory of the New York Botanical Garden and specimens of the plant have been deposited in the herbarium of that institution.

I was unable to follow the origin and development of the archesporium satisfactorily and therefore begin my discussion with the functional megaspore, which is very conspicuous and located some four to six layers of cells below the surface of the ovule (*figure 1*). It grows rapidly and develops into the normal eight-nucleate sac (*figures 2, 3, 4*). In the four-nucleate stage (*figure 3*) the sac is considerably larger at the synergid than at the antipodal end and agrees quite well in shape with Wiegand's figure 19. The two nuclei of the synergid end are placed at right angles to the long axis of the sac and ovule, while the two in the antipodal region are placed in the same direction as the long axis. The nuclei of the synergid end divide a little in advance of those of the antipodal end. A number of preparations in this stage were examined but in no case was there a common membrane around the cells in the synergid end previous to fertilization as described by Wiegand. In the eight-nucleate stage the nuclei are perfectly clear and well defined (*figure 4*). The two synergids and egg are quite large, and each is surrounded by a delicate membrane. The three antipodals are relatively large and have well-defined walls. They were never observed in a well-defined pocket as described and figured by Wiegand and by Holferty. The polar nuclei are somewhat smaller than in most plants which the writer has examined. They unite about the middle of the sac in the usual manner (*figures 4, 4a*). The fertilization of the egg was not observed but the union of the two polar and one male nucleus was observed once (*figure 4b*). Other preparations apparently showed the same thing but upon this point the writer could not be positive.

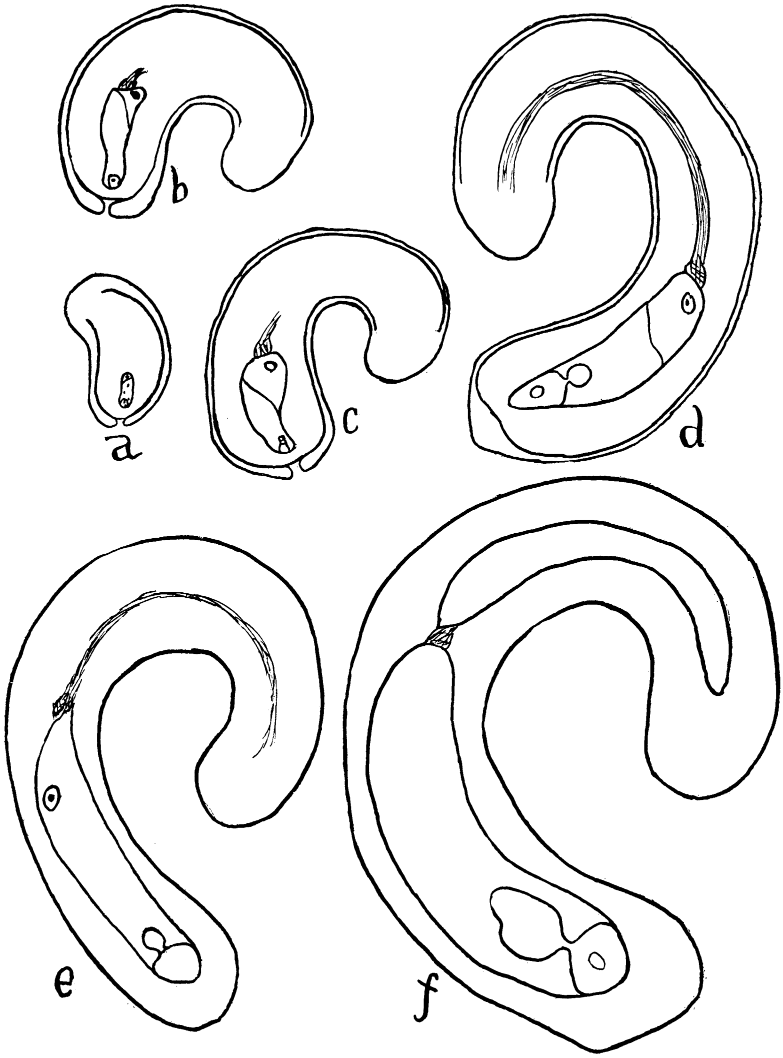
After a union of the two polar nuclei the newly formed endosperm nucleus increases in size rapidly and passes into the antipodal end of the sac (*figures 5, 6*). In the meantime the antipodal cells disintegrate and disappear entirely (*figure 6*), the young unicellular embryo (or pro-embryo) increases in size rapidly while the synergids gradually disintegrate (*figures 5, 6, 7, 8, 9*). At this time the general appearance of the sac is strikingly similar to that shown in Wiegand's figure 20.

The primary endosperm nucleus now divides into two daughter-cells which are immediately separated by the formation of a wall across the sac (*figure 7*). The daughter-nucleus on the synergid side of the wall divides rapidly and produces an abundant endosperm, which is usually non-cellular and parietal in character (*figure 12*), but occasionally becomes cellular and fills the entire sac (*figure 13*). The sac increases in size, especially in its long axis, the nucellar tissue bounding it gradually undergoing disintegration. At the same time the daughter-nucleus in the antipodal end, which, in accordance with my second paper on Nymphaeaceae, I shall designate as the "nucleus of the nucellar tube," increases rapidly in size and moves farther and farther from the partition-wall (*figures 9, 10, 11,* and *text-figures a–f*). This increase in size and activity continues until the embryo has reached the age indicated in *figure 22*, after which it undergoes disintegration (*figure 11*) and gradually disappears. Some time previous to this the partition separating the two ends of the sac has also disappeared.

At about the time of the disintegration of the large nucleus of the nucellar tube the endosperm is very conspicuous, consisting of large spindle-shaped cells (*figure 12*) which stain deeply and frequently contain several nucleoli and evidently are very active. In most cases they are without cell-walls and form a parietal layer one to three cells thick lining the sac, but occasionally they have cell-walls and fill the entire sac (*figure 13*). With the breaking down of the wall across the sac and disintegration of the large cell of the nucellar tube the endosperm extends into the antipodal end of the sac. Coördinate with the activity of the endosperm there is a corresponding disintegration of the nucellar cells bounding the sac.

Soon after the division of the primary endosperm-nucleus a mass of small nucellar cells may be distinguished at the antipodal end of the sac (*figure 14* and *text-figures b–f*) and from this mass of cells there extends to the chalazal region a core of elongated cells which eventually disintegrate, leaving a large third chamber which is separated from the true embryo-sac. It is probable that this sac finally becomes a part of the embryo-sac and is occupied by the cotyledonary end of the embryo.

The gradual increase in size and the modifications in the shape of the ovule and sac are shown in *text-figures a* to *f*. *Figure a* corresponds to *figure 9*; in *figure b* the sac is somewhat larger



FIGS. *a–f.* Diagrammatic drawings showing the shape and relative sizes of the embryo-sac, embryo, and ovule at various stages of their development. Also, the wall across the sac in *a, b, c, d;* the mass of small nuclear cells at the antipodal end of the sac in *b, c, d, e, f;* the core of elongated cells in *d* and *e;* and the third chamber in *f.*

and the mass of small nucellar cells is quite prominent; in *c* the sac is still larger and the embryo is in the stage corresponding to *figure 15;* in *d* both the sac and the embryo are very much larger, the embryo at this time being about the age indicated in *figure 21;*

in *e* the sac has increased somewhat in size, the partition-wall has disappeared, the large tube-nucleus has reached its maximum in both size and activity and the embryo is about the same age as in *figure 22*; in *f* the sac is very much enlarged and the new chamber at the chalazal end of the sac has developed, the embryo at this time being about the same age as in *figure 24*.

The formation of a wall across the embryo-sac separating the two daughter-nuclei formed by the first division of the primary endosperm-nucleus has been observed in many plants. It occurs in both dicotyledonous and monocotyledonous families but further studies will probably show marked differences in its behavior in these two main groups of angiosperms.

The embryo-sac of *Alisma Plantago* (now known as *Alisma Plantago-aquatica*) as described by Schaffner (12) corresponds in most respects to that of *Potamogeton lucens*, although he did not observe the formation of a wall after the division of the primary nucleus. However, in his later work on *Sagittaria variabilis* (13), (now known as *Sagittaria latifolia*) he describes a sac which corresponds remarkably well to that of *P. lucens*, with the exception that the antipodals are more persistent and that the nucleus of the nucellar tube has a tendency to fragment.* It is possible that further study of *Alisma Plantago-aquatica* will also show the formation of a wall across the sac. My own studies on Nymphaeaceae show the same formation of a wall across the sac separating the two daughter-nuclei of the primary endosperm-nucleus, the daughter-nucleus in the synergid end of the sac giving rise to the endosperm and the daughter-nucleus in the antipodal end passing into a tube or saccular structure (differing somewhat in different genera) formed by disintegration of the nucellar tissue. The behavior of this nucleus of the nucellar tube of the genus *Nymphaea* was more nearly like that of *Potamogeton lucens* than that of any other genus. In fact the general appearance, history, and behavior of these structures in *P. lucens* and in *Nymphaea* are strikingly similar. Johnson (10) describes a similar condition in *Saururus cernuus*, which is very similar to that described by me for

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*Schaffner's studies on *S. variabilis* were verified by my own studies on *S. lancifolia* with the exception that I found the antipodals of *S. lancifolia* not so persistent as in *S. variabilis*.

Castalia ampla in my paper on Cuban Nymphaeaceae (5). Coker (3) describes a somewhat similar condition for certain of the Pontederiaceae except that he describes the daughter-nucleus in the antipodal end of the sac as going through a series of divisions to form an endosperm. Campbell (1) reports the presence of a large cell in the antipodal end of the embryo-sacs of *Naias flexilis* and *Zannichellia palustris* but did not determine its origin in either case. However, he states that this cell does not divide, but that in *Zannichellia palustris* "it looked as if it were undergoing disintegration," and that in both plants the endosperm arises in the synergid end of the sac. Hall (8) in his studies on *Limnocharis emarginata* reports a single antipodal cell and a single polar cell which is formed in the micropylar end of the sac; this single polar cell divides and behaves in the same manner as the primary endosperm in the Nymphaeaceae, *Sagittaria*, and *Potamogeton lucens*. This embryo-sac is so remarkable in character and so unlike any other known at this time, while the behavior of the polar nucleus is so similar to the primary endosperm of the plant just referred to, that one is justified in saying that the union of the two polar nuclei may have been overlooked. Wiegand (14) in his studies of *Potamogeton foliosus* describes a peculiar seven-nucleated sac in which but three nuclei (the egg and the two synergids) are formed at the micropylar end of the sac, the polar nucleus from the antipodal end of the sac dividing and behaving similarly to the primary endosperm-nucleus in Nymphaeaceae, *Sagittaria*, and *P. lucens*. Holferty (9) in his studies of *Potamogeton natans* describes a normal eight-nucleated sac. He failed to find a wall across the sac at any stage of its history. He did not trace the development of the endosperm but reports a very large nucleus near the antipodal end of the sac, concerning which he says "Its origin could not be determined, but it seems reasonable to consider it a derivative of the primary endosperm-nucleus, and possibly the lower nucleus of the first division, as in *Sagittaria* and *Potamogeton pauciflorus*." In the light of these later studies it seems possible that Wiegand may have overlooked the formation of the eight-nucleate sac. Aside from the fact that the antipodal cells of *Potamogeton foliosus* are evidently more persistent than those in *P. lucens*, his figure 20 corresponds quite well with *figures 5* and *6* of this paper, his figure 21 with my *figure 7*, his figure 23 with my *figure 8*, and his figure 24 with my *figure 9*. It is well known that there may be considerable variation between genera of the same family and also some variations between species of the same genus. This question of the variation and constancy of characters between closely related species, genera, and families is of sufficient importance to demand the attention of students of this subject.

That this large nucleus of the nucellar tube performs a very important function in the nourishment of the endosperm and embryo appears self-evident at this stage of our knowledge. The writer has previously discussed this phase of the subject in papers on Nymphaeaceae (4, 5). Its morphological significance is somewhat uncertain. In my first paper on Nymphaeaceae (4) I expressed the opinion that this might be of some importance in determining the close relationship of the Nymphaeaceae with monocotyledonous plants in the series Helobiae. The phylogenetic importance of these morphological characters was denied by Johnson (11) but since that time the family Piperaceae, on which he made his studies, has been placed by the taxonomist as the lowest of the dicotyledonous families. The writer believes that we do not have sufficient data to draw very definite conclusions but wishes to emphasize the importance of further studies in these families.

THE EMBRYO

The general development of the embryo is in accordance with the *Alisma* type and bears a very striking resemblance to the embryo of *Sagittaria variabilis*. The young embryo increases in size but is very slow in undergoing its first division (*figures 5, 6, 9*, and *text-figures a, b, c*). A comparison of figures indicates that the first division of the embryos of *Potamogeton foliosus* and *S. variabilis* occurs earlier than in the embryo of *P. lucens*. After the first division the basal cell grows rapidly and forms a very thick cell-wall and is very similar to the basal cell of *Sparganium*, *Zannichellia*, *Naias*, *Triglochin*, *Limnocharis*, and *Potamogeton foliosus* and *P. natans* (*figures 15, 18, 23*). It contains an abundance of protoplasm, stains deeply, and gives every evidence of great activity until the appearance of the cotyledon, when it first shows signs of disintegration.

The number of cells in acropetal succession may be six in number. When three cells are formed the apical cell divides by the formation of two longitudinal walls at right angles (*figure 15*) and this is followed by cross and longitudinal divisions of the second and third cells (*figures 16, 17, 19, 20, 21*). Thus far the formation of the embryo is in harmony with the descriptions given by Wiegand and Holferty for *P. foliosus* and *P. natans*.

The further development of the embryo shows some variations at this point, in some cases showing three well-defined segments (*figures 18, 19, 21*), while in others it showed only two, as indicated in *figure 20*. The writer is unable to say positively whether the formation of the parts is strictly in accordance with the *Alisma* type or whether there is a variation as described by Campbell (1) for *Zannichellia*, but is inclined to the former view, which is assumed to be true in the further discussion of this subject. It will be noted at this time that *figure 20* corresponds quite well to Wiegand's figure 26.

The apical cell, as previously stated, divides and eventually gives rise to the cotyledon. The second cell divides by a cross-wall; of these two daughter-cells the one next to the apical cell divides, forming a second segment from which is derived the apex of the stem. The other daughter-cell forms the third segment and part of the suspensor by which the embryo is attached to the large basal cell. From this third segment are derived the hypocotyl and the root-tip. These three segments are shown in *figures 18, 19*, and *21*. Cell *a* of *figures 18, 20*, and *21* divides transversely into cells *a* and *a'* of *figure 22*. Cell *a* of *figure 22* evidently forms in part or entirely the dermatogen of the root-tip (*figures 23, 24*), while *a'* of *figure 22* divides to form cells *a'* and *a''* of *figure 23*. Cell *a'* of *figure 23* now undergoes division to form the calyptrogen, as shown in *figure 24*, while cell *a''* becomes a part of the suspensor. Shortly after this, the plerome and periblem show indications of differentiation (*figure 24*).

As previously stated, with the appearance of the cotyledon (*figure 23*) the large vesicular basal cell of the suspensor shows signs of disintegration. The suspensor is always delicate and the embryo even in its early stages is frequently found separated from the basal cell.

SUMMARY

1. The formation of the embryo is regular and typical.

2. The primary endosperm-nucleus divides and the two daughter-nuclei are separated by a wall. The one in the synergid end of the sac gives rise to the endosperm while the one in the antipodal end grows rapidly, is very active, and moves downward into an extension of the sac formed by the disintegration of the nucellar tissue, where it finally undergoes disintegration.

3. The endosperm is conspicuous, usually parietal and nuclear, without cell-walls.

4. The embryo follows the *Alisma* type in its development.

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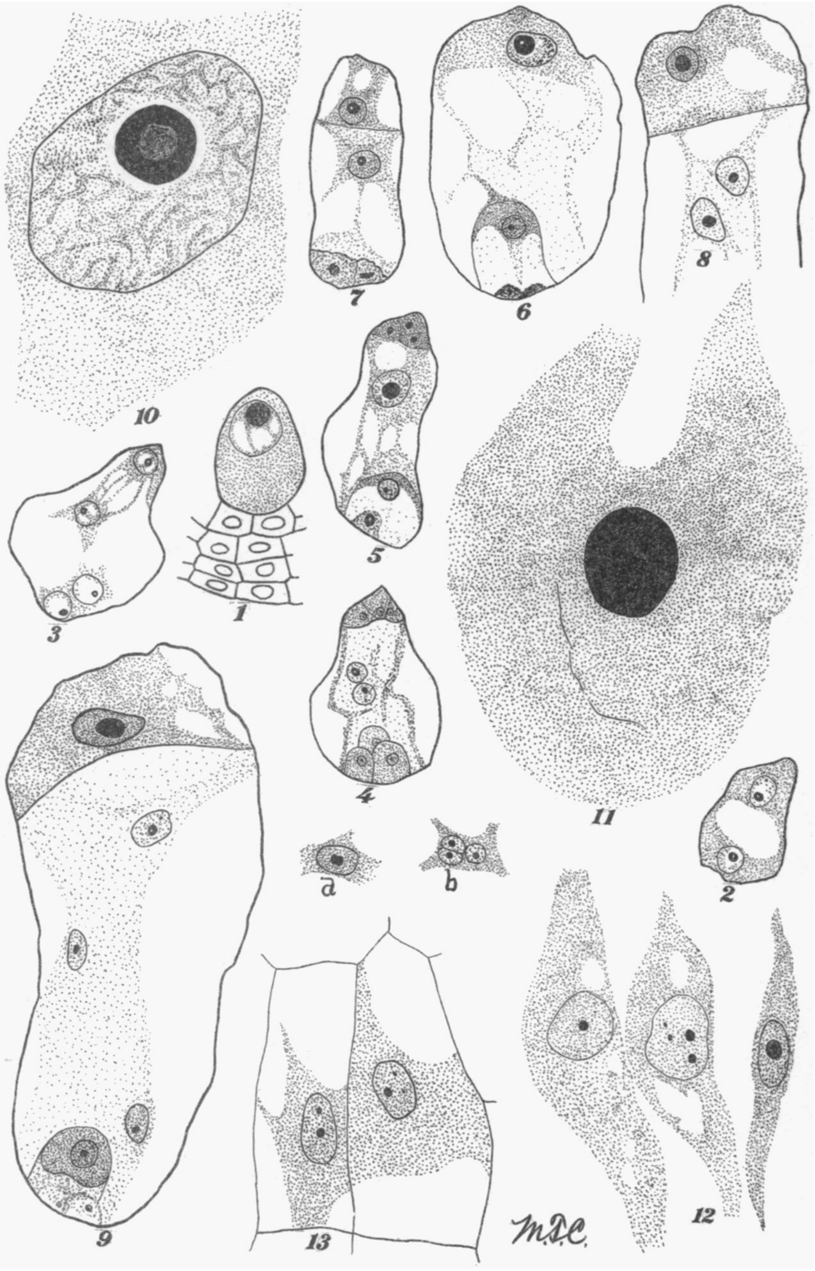
Explanation of plates 9 and 10

Figures 1 to 13 were made with Bausch & Lomb 1-inch eye-piece and 1/12 oil-immersion objective. Figures 14 to 24 were made with same eye-piece and 1/6 objective. All have been reduced somewhat more than one half in reproduction.

FIG. 1. Functional megaspore.
FIG. 2. Two-nucleate sac.
FIG. 3. Four-nucleate sac.
FIG. 4. Eight-nucleate sac.
FIG. 4a. Complete union of the polar nuclei.
FIG. 4b. Union of polar nuclei and male nucleus.
FIG. 5. Sac soon after fertilization.
FIG. 6. Sac soon after disintegration of the antipodal cells.
FIG. 7. Sac soon after first division of the primary endosperm-nucleus.
FIG. 8. Sac soon after first division of the nucleus in the antipodal end of the sac.
FIG. 9. Sac showing increase in endosperm growth of the nucellar tube nucleus.
FIG. 10. Nucellar tube nucleus at its maximum in size and activity.
FIG. 11. Nucellar tube undergoing disintegration.
FIG. 12. Typical endosperm-cell without walls.
FIG. 13. Unusual endosperm-cell with walls.
FIG. 14. Mass of nucellar cells at the antipodal end of the embryo-sac.
FIG. 15. Young embryo after first longitudinal division of the apical cell.
FIG. 16. Young embryo slightly older than in Fig. 15.
FIG. 17. Young embryo slightly older than in Fig. 15.
FIG. 18. Young embryo, showing three segments.
FIG. 19. Young embryo, showing three segments, slightly older than in Fig. 18.
FIG. 20. Young embryo, rather unusual form.
FIG. 21. Spherical embryo, showing three segments.
FIG. 22. Spherical embryo, showing three segments, slightly older than in Fig. 21.
FIG. 23. Embryo, showing the cotyledon and also the large vesicular basal cell in first stages of disintegration.
FIG. 24. Embryo, showing differentiation of tissues.



EMBRYOLOGY OF POTAMOGETON LUCENS

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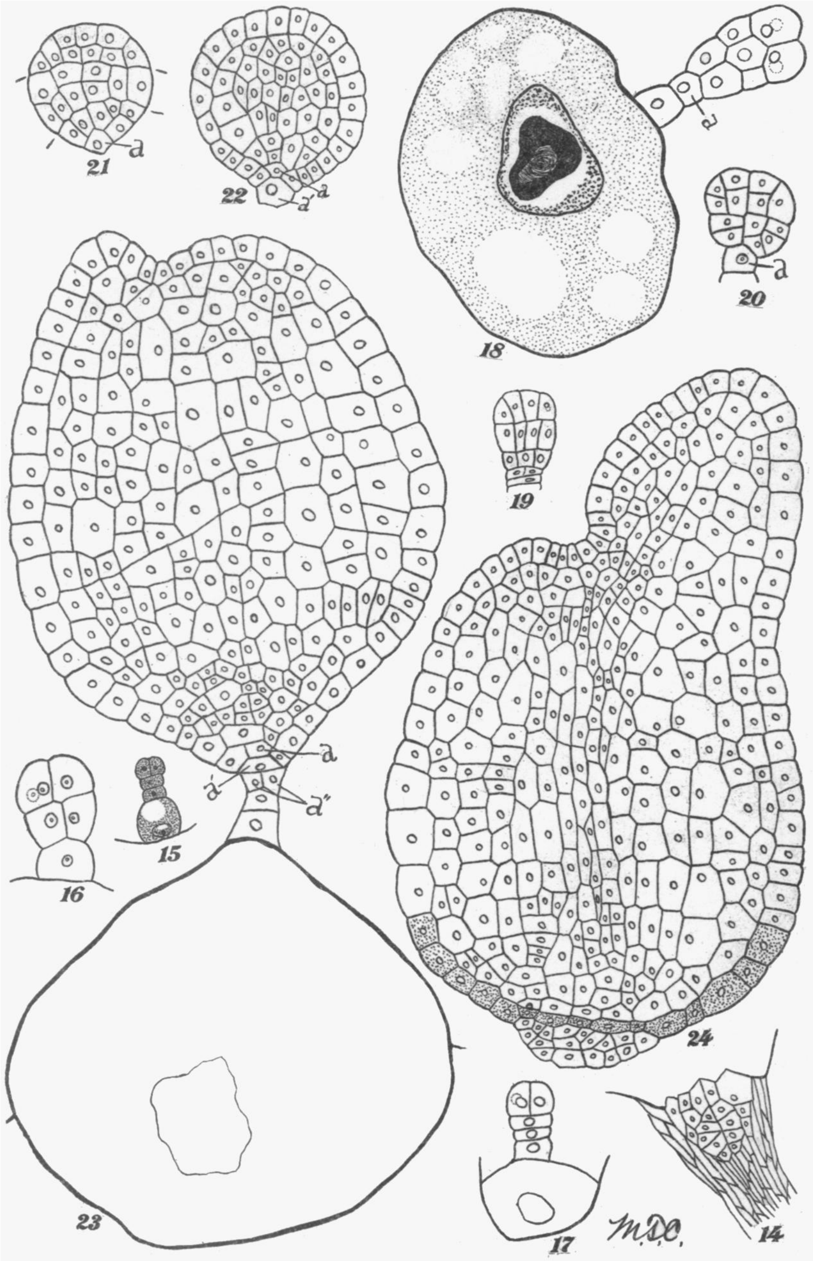

EMBRYOLOGY OF POTAMOGETON LUCENS